Organisms as sacks of chemical reactions

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Every living thing is made of chemicals (which are made up of atoms[1]). Perhaps more to the point, we are made of chemical reactions, endless chains of chemical reactions where the product of one is a reactant to another. You have likely seen the citric acid or Krebs cycle, photosynthesis, protein synthesis, or any number of other reactions involved in life. That stuff[2] is happening inside of us right now, as I write and you read. These reactions are happening all the time. That, in a very real sense, is life: self-perpetuating, self-organizing chemical reactions. We will not worry ourselves with the details—this is a general ecology class after all, and I always forget the details—but just this basic idea can yield some interesting perspectives.

[1] The major ones, some 98% of living matter, are C, H, N, O, P, and S, or CHNOPS. But smaller amounts of so-called micronutrients are also needed, depending on the organisms. These include : Na, Mg, K, Ca, Cl, Mn, Fe, Cu, Zi, I, K, Fe. Google them to find out their various roles. They are quite interesting!

[2] Well, not photosynthesis! I mean, if it, please let me know and we can write a major Science paper!

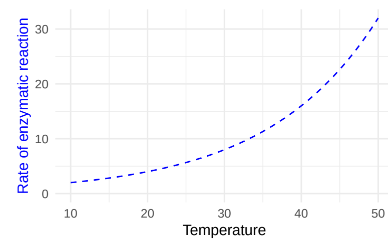
Biology is temperature-dependent

One way to increase the rate of a chemical reaction is to add heat. With heat, chemicals bounce around faster and so come into contact more frequently[3]. The added energy also speeds reactions by providing the activation energy required in endothermic and even some ectothermic reactions. All of which is to say, reactions go faster at warmer temperatures. What are the consequences? Let's consider two:

[3] Hmm…is this a useful analogy with susceptible and infected hosts interacting to cause more infections?

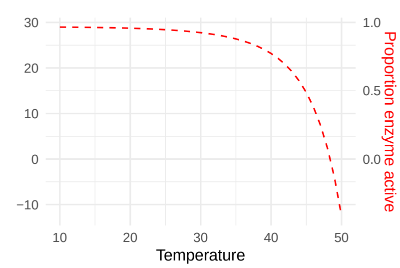
Thermal optima

Rates of chemical reactions increase *exponentially* with temperature[4]. As a quick rule of thumb, if the temperature is increased by $10°C$, the rate of the reaction often doubles. So the rate of reactions, even enzymatic reactions such as those involved in metabolism or muscle contractions or most any other biochemical process, tends to increase like the blue line on the graph to the right.

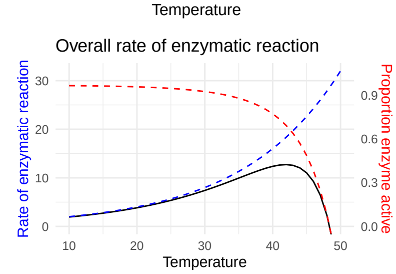


[4] If you wonder why, look up the Arrhenius equation…yet another exponential model, but this one describes the "rate constant" of a chemical reaction.

Your intuition is probably quietly screaming at you right now, saying, "yeah, but…!" And your intuition is right. This accelerating relationship between the rate of a reaction and temperature cannot go on forever. At some point, everything catches on fire and you get soot rather than a muscle contraction, right? Well, well before that we run into limits. Most biochemical reactions involve enzymes and enzymes eventually fall apart or "denature." (The same can happen to some of the chemical reactants, too.) We might graph the rate of denaturing as the red line on the graph to the right.



When we put these rates together we get an overall rate of the reaction, with a clear peak. This peak is the "optimal" temperature in that it maximizes the overall rate for that reaction. What is striking is that the optimal temperature for many biochemical reactions in an organism are pretty similar[5]. What this means is that a organisms tend to have thermal optimums that relate to these biochemical optimums. Running speed of a lizard? Yes, it has a thermal optimum. A mosquito



[5] Why would that be? Consider what would happen if they were all very different.

digesting a bloodmeal? That, too, happens fastest at a particular temperature. Most all of biology has some small-ish range of temperatures where we perform best. We humans often do not think about this simply because our physiology works so hard to maintain our body temperature very near our thermal optimum. But trust me, if our core temperature drops a bit, so does our metabolism, just as we would expect[6].

So why do organisms have narrower ranges of temperatures in which they thrive compared to what they can survive? Look to the thermal optima of their chemical reactions[7]!

[6] This also hints at a secret weapon of ectothermic poikilotherms, those things like amphibians and reptiles and some fish that not only get most of their heat from the world around them, but can let their body temperature vary a great deal: they can regulate their metabolism by changing their body temperature. Not food? Why not cool off and wait it out? We ridiculous endothermic homeotherms cannot pull off *that* trick!

[7] I am overselling this a bit. While the logic holds and there are many examples of temperature-dependent processes from the small (e.g., metabolism) to the large (e.g., speed), there are many other factors that end up affecting temperature-function relationships at the organism level, such as compensatory adaptations to nutrition. That is, we need to be cautious about scaling up these mechanisms to far without some care.

Temperature-dependent rates of development

Temperature-dependent rates and thermal optima also extend to development. Consider the process of going from an egg to a hatchling to a juvenile to an awkward, gangly pubescent teenager equivalent to a mature adult, or similarly a seed to seedling to small tree to mature tree. All of these steps are the result of a series of chemical reactions. Because these reactions tend to go faster at warmer temperatures, the time it takes to get to a particular developmental milestone (e.g., hatching or sprouting) tends to be shorter at warmer temperatures[8]. And while these rates increase more-or-less exponentially over a wide range of temperatures, most organisms do not live, or at least develop, over a terribly wide range of temperatures. Over this narrower range we might be forgiven for thinking that the rate is sort of linear. Let's run with this linear relationship between temperature and rates of development. What are the consequences?

[8] Yes, only up to a point.

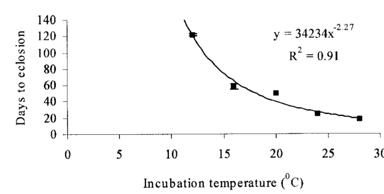


Figure 1: Time to eclosion (hatching) for black legged ticks. From Ogden et al. 2004. Journal of Medical Entomology 41:622-633.

First, if we were to raise, say, ticks or mosquitoes from eggs at one of a range of temperatures, we would see that the time to some developmental milestone declines rapidly with increasing temperature at first, but that change slows down. Indeed, this is a hyperbolic relationship where the time to the milestone is just one over the rate of development, which we just noted increases approximately linearly with temperature. That is, $T = 1/d_t$, where d_t is the development rate at temperature t and T is the time to the milestone. Clear? No? OK, let's try an analogy.

Imagine you are driving to the West Side. Let's say it is a 300 mile journey. You could drive the whole way at 60 miles per hour and it would take 300 miles/60 mph = 5 hours or you could drive at 90 mph and it would take 300 miles/90 mph = 3 hours 20 minutes. I you are a very slow driver moving at 30 mph this trip would take 10 hours! A graph of the time it takes to get to your destination, your milestone if you will, follows the same shape as the development graph, above.

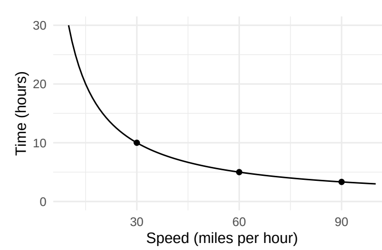


Figure 2: Time to drive to the West Side as a function of speed.

This analogy is important for another reason, because it helps us notice that we do not need to drive (or develop) at a constant rate, but rather accumulate speed (or temperature) and thus miles driven (or steps in development) to get to our destination. We might drive at 60 for a bit while we get through Colfax and then floor it on I-90 until we get snarled in traffic near Seattle. Similarly, development might be speeding along on warm days and going slower on cools ones. In biology we call this the "degree-day" model of development[9], where we can estimate the accumulation of temperature as a proxy for the accumulation of development to some developmental milestone.

[9] Sort of like the speed-hour model of travel

This sort of model is very common in farming, but is also very useful for thinking vector ecology. Ticks and mosquitoes take a certain number of degree days[10] to complete their development into the next developmental stage, lay eggs, or even digest a bloodmeal. What's cool about this is that we can figure out how many generations we might have in an area as a function of that area's typical temperatures. It can even explain why, say, ticks are not found too far north: it is simply too cold for them to complete their development before they would run out of energy or freeze to death.

[10] Often above some threshold temperature where there is no development. Zero Celsius is pretty cold, after all!

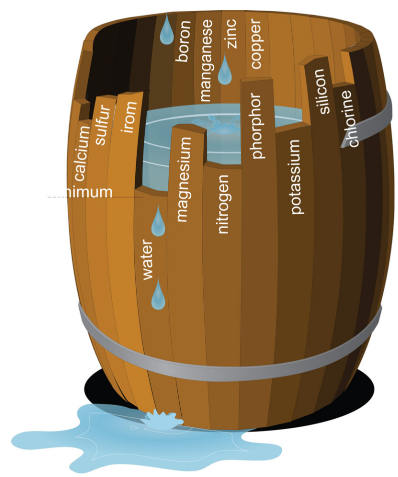
Rates are controlled by the most-limiting reagent

In addition to increasing temperatures or adding catalysts (e.g., enzymes), one way to speed a chemical reaction is to increase the concentration of the reactants. This is also true, to an extent, in biochemical reactions. Or more to the point, if a reactant is missing, it slows the rate of the reaction[11]. But what is important to remember about biochemical reactions is that reactions are chained together such that the product of one is the reactant of another. So slowing down one reaction can slow down others[12].

[11] A plant cannot fix CO_2 with photosynthesis if there is no more CO_2!

[12] If nitrogen is limiting, it slows down production of amino acids, which slows down protein synthesis, which slows down growth or repair of myriad cell structures, and so on.

What is important to remember is the rate of a reaction is limited by the reactant that is in the most limited supply. What this means is that if nitrogen is limiting, adding more phosphorus is unlikely to speed up the reaction(s). But it also means that adding nitrogen speeds up the reaction only until something else becomes limiting. This is often called Liebig's law of the minimum[13] or Liebig's barrel, because, like the water level in a barrel is limited by the shortest stave, the growth of a plant or animal is limited by the nutrient in shortest supply. Me, I like to think about this as the law of the movie theater popcorn. Sure, a small popcorn is lovely and a medium increases my happiness, but I never get the super large size, even if it is just 50 cents more, because I know my happiness is no longer limited by popcorn, but probably by my need for water given all the salty popcorn I just ate! In any case, given this insight is it any surprise that one line of defense against invading pathogenic bacteria is for our bodies to sequester nutrients that likely limit bacterial growth?



[13] A prime example of Stigler's law of eponymy.

An organism's stoichiometry can help explain where and when it flourishes

If we follow Liebig's law of the minimum a short step further, we might note that fertilizers, for instance, might be most effective if they included several of the commonly limiting nutrients. And they might be more effective still if they contained the right *ratios* of these limiting nutrients. Why is this? Well in a word, stoichiometry. In more words, chemical reactions use nutrients in particular ratios. For instance, photosynthesis takes six CO_2 molecules and 12 H_2O molecules, plus some light and fancy enzymes, to make one sugar ($(C_6H_2)_6$) and some oxygen and water. That is more O's than C's in this particular reaction. Similarly, while amino acids require nitrogen, they have a lot more carbon and oxygen atoms in them.

More broadly, we can think about *ecological* stoichiometry, where we consider what the whole organism needs and uses, as opposed to particular chemical reactions. We need nitrogen not just for amino acids, but also RNA and DNA. We need phosphorus in our nucleic acids, but also phospholipids, and ATP, along with structural elements in bones. We can sort of set aside the issue of where the N's and P's go and just think about how many N's a body needs relative to the P's, and if we get this ratio right we tend to maximize the rates of the organisms's chemical reactions.

This ecological stoichiometry is a relatively new idea and undertaking, and it is not entirely clear how far we can run with it, but there are some very interesting places where it clearly works. For instance, rapid growth requires the production of a lot of nucleic acids, ATPs, and ribosomes, which require a lot of phosphorus. Thus, we find, at least in some settings like zooplankton, that fast-growing species and life stages tend to grow best with more P than N (or, equivalently, lower N:P ratios) than slower-growing species and stages. Indeed, lab experiments demonstrated that one could manipulate the relative dominance of copepods (cylopoid crustrations) versus *Daphnia* (cladocerans) by changing the elemental ratios in the food they were provided. The ideas have been promoted in all sorts of areas (e.g., cancer research), but again, it is not always clear that what is true at the small scale is necessarily important at the large.